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HISTORICAL BIOGEOGRAPHY AND LATE GLACIAL ORIGIN OF THE FRESHWATER PEARLY MUSSEL (BIVALVIA: UNIONIDAE) FAUNAS OF LAKE ERIE, NORTH AMERICA

Daniel L. Graf[1]

Abstract. The objectives of this paper are two-fold: (1) to review the historical distributions of the freshwater pearly mussels (Bivalvia: Unionidae) of the Lake Erie Basin of North America and (2) to test the traditional hypothesis that all Ohio Basin mussels present in Lake Erie migrated there during the stand of Glacial Lake Maumee (between 14,400 and 13,900 years ago). Forty-four mussel species occur in the Lake Erie Basin, and these are herein divided into five faunas based upon their shared distribution patterns in the Great Lakes: the Great Lakes Fauna, the Central Great Lakes Fauna, the Erie-Michigan Fauna, the Erie Fauna, and the Northern Atlantic Slope Fauna. The spatial and temporal distributions of those faunas do not support the Glacial Lake

[1]Department of Biology and Museum of Zoology, University of Michigan, Ann Arbor, Michigan 48109, U.S.A.
Current Address: Academy of Natural Sciences, 1900 Benjamin Franklin Parkway, Philadelphia, Pennsylvania 19103, U.S.A.

Maumee dispersal hypothesis; this is corroborated by the vicariant distributions of the Great Lakes fishes. It is concluded that, although some species may have colonized Lake Erie through Glacial Lake Maumee, many other species arrived perhaps as recently as Nipissing time (6000 to 4000 years ago).

Keywords: Unionidae, Great Lakes, Biogeography, Glacial Lake Maumee.

Introduction

"If the theory of the Ice Age as held by most glacialists is a true one I think it will fully explain the present remarkable distribution of these extra-limital Mississippi Valley Naiades." -- Charles T. Simpson (1896)

Near the beginning of the 20th century, when North American malacologists began to run out of new species of naiades, or freshwater mussels (Bivalvia: Unionidae), to describe, they turned their energies toward taxonomic syntheses and biogeography (Simpson, 1900, 1914; Ortmann, 1912, 1919; Frierson, 1927). Of special interest was the mussel fauna of the Laurentian Great Lakes (Simpson, 1896; Walker, 1913; Ortmann, 1924), a molluscan community with affinities to the upper Mississippi River, the Ohio River, and, to a lesser extent, the northern Atlantic Slope (Johnson, 1980). The "metropolis" of this province, according to Walker (1913: 18), was Lake Erie. He listed 39 species as inhabitants of that basin, but it has more recently been suggested that the actual tally may be higher (*e.g.*, van der Schalie, 1945; Johnson, 1980). Due to the disagreement among recent studies, a thorough re-evaluation of the freshwater mussel fauna of the Great Lakes is long overdue. My objectives are to determine the historical freshwater mussel assemblage of the Lake Erie Basin, their distributions within and around the basin, and to test previous hypotheses of the origin of the community.

Lake Erie is situated at the junction of Michigan, Ohio, Pennsylvania, New York, and Ontario in the United States and Canada (Figure 1). The lake trends roughly west to east for roughly 400 km and averages 60 km wide, covering over 25,700 km^2. While receiving the bulk of its input from the upper Great Lakes (Lakes St. Clair, Huron, Michigan, and Superior with a total drainage area of 592,600 km^2) via the Detroit River, the local Lake Erie catchment contributes an additional 90,400 km^2. Other major rivers draining directly to the lake are the Huron, Maumee, Sandusky and Cuyahoga rivers in the United States and the Grand River of Ontario. The sole outlet for Lake Erie is the Niagara River at Buffalo, New York. During the early part of the 1800's, the construction of a series of barge canals created aquatic connections among Lake Erie, the Interior Basin, and the Atlantic Slope.

As recently as 15,000 ^{14}C-years before present (B.P.), the entire Lake Erie Basin was completely inundated by ice associated with the latest Wisconsinan glacial maximum (Mickelson *et al.*, 1983). As with all territory north of the glacial maximum, the deglaciated areas were repopulated by colonization from unglaciated refugia (Walker, 1913; Johnson, 1980; Underhill, 1989; Graf, 1997b; Graf and Underhill, 1997). As the glaciers wasted northward, meltwater was impounded between the ice margin and the height of land separating the Great Lakes from the Mississippi Basin, forming enormous glacial lakes (Teller and Clayton, 1983; Karrow and Calkin, 1985). These glacial lakes overran present-day divides and facilitated temporary confluences between recently deglaciated areas and unglaciated refugia.

A series of such lakes formed in the Lake Erie Basin, beginning with Glacial Lake Maumee (Calkin and Feenstra,

Figure 1. Map of present-day Lake Erie and adjacent basins.

1985). Ice-bounded on the north and east, Glacial Lake Maumee filled much of the present-day Maumee River Basin (Figure 2) and drained to the Ohio River via the Wabash in Indiana. Simpson (1896) and others (*e.g.*, Walker, 1913) hypothesized that this confluence between the Erie and Ohio basins allowed freshwater mussels, which are distributed by their host fishes (Johnson, 1970; Graf, 1997b), to colonize Glacial Lake Maumee through the unglaciated Wabash basin.

With the exception of Ortmann's (1924) limited discussion (see below), this theory, the Glacial Lake Maumee dispersal hypothesis, has not been tested.

Historical biogeographic hypotheses are inherently difficult to appraise since they generally lie outside the realm of experimentation (Brown and Lomolino, 1998). Instead, we must assess how well a hypothesis is corroborated by several lines of evidence and base our conclusions upon falsifiable predictions of the expected data patterns. The Glacial Lake Maumee dispersal hypothesis of the origin of the Lake Erie mussel fauna should not only be consistent with the known distribution of those taxa within the Lake Erie Basin, but also with their distributions in adjacent basins, the unionid fossil record of the region, vicariance with other aquatic taxa with similar dispersal ability (*i.e.*, the fish), and the Late Quaternary geology of the central Great Lakes.

Ortmann (1924) elaborated the Glacial Lake Maumee hypothesis of the origin of Lake Erie unionids to explain the once-puzzling distribution of mussel 'forms' among the tributaries of the basin and in the lake itself. Freshwater mussels colonized the basin through Glacial Lake Maumee, but the lake itself was hypothesized to be a barrier to river species. Since the river 'forms' could only be dispersed through continuous lotic habitats, he theorized that during a "Nipissing" low-water stand in the Lake Erie Basin, a continuous river system existed that allowed unionid dispersal throughout (Ortmann, 1924: figure 2). It is important to note that (1) Ortmann (1924) considered this theory sufficient to explain the origin of all Ohio basin mussels in the Lake Erie drainage, and (2) this interpretation has been upheld in subsequent reviews (*e.g.*, Grier, 1919; van der Schalie, 1945; Stansbery, 1961; Johnson, 1980; Clarke and Stansbery, 1988; Strayer *et al.*, 1991). The individual 'forms,' however, are no longer recognized as valid taxonomic units (Williams *et al.*, 1993).

The Glacial Lake Maumee hypothesis can now be more precisely stated based upon our improved understanding of

Figure 2. (opposite page) Two phases in the Quaternary evolution of the central Great Lakes. Arrows indicate the direction of flow. 14,000 B.P. marks the extent of Glacial Lake Maumee (14,400 B.P. to 13,900 B.P.) in the Lake Erie Basin. Glacial Lake Maumee drained via the Wabash River, its outlet near the point of present-day Ft. Wayne, Indiana. At the same time, meltwater accumulating in the Huron Basin drained west via the Grand River to the Michigan Basin and from there to the upper Mississippi Basin. By 13,600 B.P., ice in the Huron Basin had wasted far enough north to open lower outlets in the Lake Erie Basin. Lowering of the lake level ended the outflow of meltwater to the Wabash and led to drainage of the Erie and Huron basins (*i.e.*, Glacial Lake Arkona) through the Grand River to the glacial lake in the Michigan Basin.

The lower frame of the figure also depicts the hypothetical arrangement of the Wabash, St. Joseph, St. Marys, and Maumee rivers suggested by Bleuer and Moore (1972).

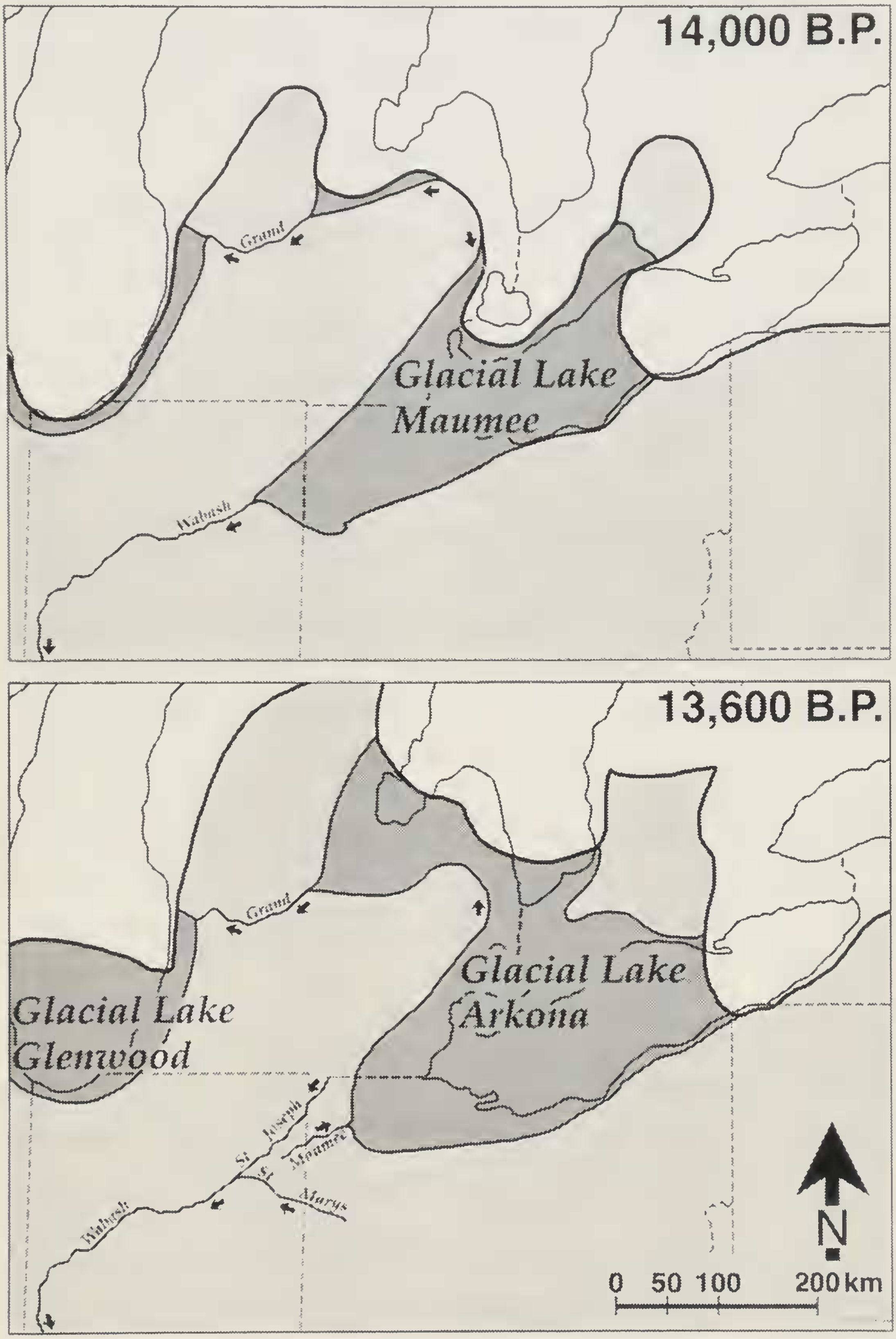
14,000 B.P.
Grand
Glacial Lake
Maumee
Wabash
13,600 B.P.
Grand
Glacial Lake
Glenwood
Glacial Lake
Arkona
St. Joseph
St. Marys
Maumee
Wabash
N
0 50 100 200 km

Figure 2.

Late Quaternary history in the Great Lakes region. Ortmann would have had available to him only the now classic geological studies that lacked the benefit of radiocarbon dating (*e.g.*, Leverett, 1902; Leverett and Taylor, 1915). Improved synopses of eastern North American glacial history are now available that provide reasonably accurate ^{14}C dates for the various glacial maxima and lake levels (*e.g.*, Porter, 1983; Karrow and Calkin, 1985). Glacial Lake Maumee drained via the Wabash from approximately 14,400 to 13,900 B.P. (Figure 2). After that period, a series of lower lake levels occupied the Erie basin, draining either to Lake Michigan via the westward flowing Grand-Saginaw Channel (Figure 2) or to the east through Lake Ontario or Mohawk outlets in New York. Moreover, the low-water stage referred to by Ortmann (1924) was not a Nipissing (6000 to 4000 B.P.) event but probably occurred during the period of Lake Ypsilanti (13,500 to 13,000 B.P.) (Calkin and Feenstra, 1985: Figure 2). Therefore, according to the Glacial Lake Maumee hypothesis, the Ohio Basin Unionidae colonized the Lake Erie Basin before 13,900 years ago (*i.e.*, before the Maumee-Wabash connection was permanently severed).

For this restatement of the classic Glacial Lake Maumee dispersal hypothesis, I have derived three conditional predictions. These are listed in Table 1. The hypothesis that the Maumee-Wabash Channel was the source of *all* Ohio Basin freshwater mussels in Lake Erie is a bold hypothesis (in the Popperian sense) and is clearly *rejectable*. That is not to say *a priori* that the Glacial Lake Maumee dispersal hypothesis is false, only that it is falsifiable. It is the aim of this study to test the predictions listed in Table 1 and the viability of the long-standing Glacial Lake Maumee hypothesis of mussel distribution.

TABLE 1. CONDITIONAL PREDICTIONS DERIVED FROM THE GLACIAL LAKE MAUMEE HYPOTHESIS.

If all Ohio Basin freshwater mussels now present in Lake Erie entered the Glacial Lake Maumee Basin through the Wabash River, then

1. they all should have similar distributions in adjacent basins (*i.e.*, all Lake Erie mussels should also be found in the Lake Huron basin). There has been a continuous, aquatic connection between the Erie and Huron basins via Lake St. Clair for nearly 14,000 B.P. (Figure 1).

2. the fossil record should not be biased towards any particular assemblage (*i.e.*, fossiliferous Late Quaternary strata should bear representatives from each of the five freshwater mussel distributional faunas of Table 3). Thus, even if a mussel fauna is absent from Lake Huron, there should be fossil evidence of its presence in the central Great Lakes region dating from soon after the closure of the Maumee-Wabash Channel.

3. their hosts should also have colonized the basin via the same route (*i.e.*, the distributions of the fishes should also reflect Prediction 1). The distributions of other aquatic taxa (microcrustaceans, amphibians, most gastropods, *etc.*) are irrelevant as their vagility is not solely aquatic.

Methods and Rationale

Data to test each of the conditional predictions of the Glacial Lake Maumee hypothesis (Table 1) were principally derived from the published record. A survey of the relevant literature (Table 2) was used to infer the historical distributions of freshwater mussels reported from Lake Erie and the surrounding watersheds: Lake St. Clair, Lake Huron, the southern peninsula portion of Lake Michigan, and the adjacent streams of the Interior Basin (Figure 1). It was not the objective of my literature review to list every record for every species in every sub-basin of the central Great Lakes. As many of the species records are ambiguous or incomplete, the extensive collection of the University of Michigan Museum of Zoology (UMMZ), Ann Arbor, Michigan, was also examined for corroborating voucher specimens. The unionid nomenclature follows Williams *et al.* (1993), and figures of shells can be found in Burch (1975) and Cummings and Mayer (1992).

Those unionids with similar distributions were grouped into "faunas" (*sensu* Graf, 1997a, 1997b). Freshwater mussels of the same fauna are hypothesized to share similar modes and tempos of dispersal into the Lake Erie Basin. In order to reconstruct the migration of the Unionidae into the central Great Lakes with these data, it is necessary to assume that freshwater mussels require aquatic connections for dispersal. As larvae, unionids are parasitic upon specific host fish (or an amphibian in the case of *Simpsonaias ambigua*) (Coker *et al.*, 1921; Kat, 1984), and this is the only means of long-range mussel distribution (see Graf, 1998 and references therein). It has been argued that mussels might be distributed across drainage divides by birds, but this is highly unlikely (see discussions in van der Schalie, 1939; Johnson, 1970; and Graf, 1997b). There is no evidence of human introduction of freshwater pearly

TABLE 2. LITERATURE UTILIZED TO ESTABLISH HISTORICAL MUSSEL DISTRIBUTIONS IN LAKE ERIE AND ADJACENT BASINS.

Great Lakes (generally). Ortmann (1919), Goodrich & van der Schalie (1932), Burch (1975), Mackie *et al.* (1980), Johnson (1980), Clarke (1981).

Lake Erie Basin. Walker (1913), Ortmann (1924), Grier (1918, 1919, 1920a, 1920b), van der Schalie (1938, 1970), Matteson (1948), Stansbery (1961), Stansbery & Stein (1962), Johnson (1978), Strayer (1979, 1990; *et al.*, 1991), Masteller *et al.* (1993), Schloesser *et al.* (1996, 1998), and Metcalfe-Smith *et al.* (1998).

Maumee River Basin. Wilson and Clark (1912), Goodrich (1914), van der Schalie (1938, 1945), Clark (1944, 1977), and Strayer (1979).

Lake Michigan Basin. van der Schalie (1936, 1941).

Lake St. Clair Basin. van der Schalie (1938), Clarke (1973), Strayer (1980), Napela *et al.* (1996), Schloesser *et al.* (1996, 1998), Metcalfe-Smith *et al.* (1998), and West *et al.* (2000).

Lake Huron Basin. Goodrich & van der Schalie (1932), Hoeh & Trdan (1984), Morris & Di Maio (1995), and Staton *et al.* (2000).

Wabash River Basin. Johnson (1980) and Cummings & Mayer (1992).

Tributaries of the upper Ohio River. Ortmann (1919, 1924), Clark (1977), Johnson (1980), and Cummings & Mayer (1992).

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mussels in the study region, although other bivalves have clearly entered the basin through anthropogenic means, *e.g.*, *Dreissena polymorpha* (Pallas, 1771) (Schloesser *et al.*, 1996, 1998; Napela *et al.*, 1996; *etc.*).

The temporal distributions of the freshwater mussels of the central Great Lakes were derived not only from the literature dealing solely with the Great Lakes (*e.g.*, Baker, 1920; Miller *et al.*, 1979, 1985; Miller and Knott, 1989) but also contiguous regions of formerly glaciated eastern North America (reviewed in Ashworth and Cvancara, 1983; Graf, 1997b). No dated fossil mussel material is available from the Lake Erie Basin.

In order to test the prediction that the vicariant pattern of fish distributions matches those of the freshwater pearly mussels, the distributions presented in various articles available in Hocutt and Wiley (1986) were consulted. Fish nomenclature follows Robins *et al.* (1991).

Results

Lake Erie Freshwater Mussels Faunas, and their Distributions in Adjacent Basins. Forty-four species of freshwater mussels occur in the Lake Erie Basin (Table 3). Johnson (1980) listed more than 50 taxa in his review, but several of those are species not supported by subsequent analyses or are nomina that have been synonymized with other Lake Erie mussels. Among the former set are *Lampsilis abrupta* and *Potamilus capax*. Neither of these has been reliably confirmed by other authors, but Johnson (1980) confined their Great Lakes distributions to the Niagara region of New York.

The synopses of Burch (1975), Johnson (1980), Mackie *et al.* (1980), Strayer (1990), and Schloesser *et al.* (1996) listed *Potamilus ohiensis* among the mussels inhabiting Lake Erie. Those observations, however, are not supported by either the literature surveyed (Table 2) nor the collections of the UMMZ (see also Watters, 1995). Early on, *Lastena ohiensis* (Rafinesque, 1820) was considered to be either unidentifiable (Ortmann and Walker, 1922) or a synonym of *Utterbackia imbecillis* (Utterback, 1915-1916; Walker, 1918). *U. imbecillis* is found in the Lake Erie Basin (Table 3) and presumably has been at least partially responsible for this confusion surrounding the distribution of *P. ohiensis* (see also Robertson and Blakeslee, 1948).

Walker (1913) and van der Schalie (1938; Goodrich and van der Schalie, 1932) reported *Fusconaia subrotunda*, *Leptodea leptodon*, *Megalonaias nervosa*, and *Obovaria retusa*, but the inclusion of those species among the Lake Erie assemblage could not be corroborated. Although further study may indeed reveal the presence of the above mentioned mussels (*i.e.*, *F. subrotunda*, *L. abrupta*, *L. leptodon*, *M. nervosa*, *O. retusa*, *P. capax*, and *P. ohiensis*) in the Lake Erie Basin, they are hereby considered erroneous (Table 3).

Both *Lampsilis fasciola* and *Epioblasma torulosa*, which occur in the Lake Erie Basin, have been erroneously cited from the Lake Michigan Basin (Goodrich and van der Schalie, 1932; Johnson, 1978, 1980). These records have not been duplicated by subsequent surveys, no supporting specimens could be found in the UMMZ, and other details of these mussels' distributions are not consistent with their presence in that basin. For the purpose of this study, those records will be considered false. Future examination, however, may corroborate their presence.

Based on their distributions in the central Great Lakes region, the freshwater mussels of the Lake Erie Basin can be divided into five faunas (Table 3). Both the (1) Great Lakes Fauna and the (2) Central Great Lakes Fauna are distributed throughout the basins surveyed. The former, however, also inhabits Lake Superior (Graf and Underhill,

TABLE 3. FRESHWATER MUSSEL FAUNAS OF THE LAKE ERIE BASIN. VOUCHER SPECIMENS FOR EACH BASIN, WHEN AVAILABLE, ARE DEPOSITED IN THE MOLLUSK DIVISION OF THE UNIVERSITY OF MICHIGAN MUSEUM OF ZOOLOGY (UMMZ). SEE TEXT FOR EXPLANATIONS OF BASINS AND FAUNAS. LM = LAKE MICHIGAN BASIN; LH = LAKE HURON BASIN; LSC = LAKE ST. CLAIR BASIN; LE = LAKE ERIE BASIN, EXCLUSIVE OF THE MAUMEE DRAINAGE; MAU = MAUMEE BASIN; WAB AND OHIO = WABASH RIVER AND THE NORTHERN, UPPER TRIBUTARIES OF THE OHIO RIVER. '+' = PRESENT; 'O' = PRESENT BUT NO UMMZ VOUCHER IS AVAILABLE; '?' = PRESUMABLY ERRONEOUS RECORD (SEE TEXT).

	other Great Lakes			Erie Subbasins		Ohio Subbasins	
Species	LM	LH	LSC	LE	Mau	Wab	Ohio
Great Lakes Fauna:							
9 species	+	+	+	+	+	+	+
Central Great Lakes Fauna:							
16 species	+	+	+	+	+	+	+
Erie-Michigan Fauna:							
(1) *Cyclonaias tuberculata* (Raf., 1820)	+		+	+	+	+	+
(2) *Toxolasma parvus* (Barnes, 1823)	+		+	+	+	+	+
(3) *Truncilla donaciformis* (Lea, 1828)	+		O	+	+	+	+
(4) *Truncilla truncata* Raf., 1820	+		+	+	+	+	+

TABLE 3 (CONT.)

Species	other Great Lakes			Erie Subbasins		Ohio Subbasins	
	LM	LH	LSC	LE	Mau	Wab	Ohio
Erie Fauna:							
(1) *Lampsilis fasciola* Raf., 1820	?	+	+	+	+	+	+
(2) *Epioblasma torulosa* (Raf., 1820)	?	O	+	+	+	+	+
(3) *Ptychobranchus fasciolaris* (Raf., 1820)		+	+	+	+	+	+
(4) *Simpsonaias ambigua* (Say, 1825)		+	+	+	+	+	+
(5) *Toxolasma lividus* (Raf., 1831)		+	+	O	+	+	
(6) *Obovaria subrotunda* (Raf., 1820)			+	+	+	+	+
(7) *Villosa fabalis* (Lea, 1831)			+	+	+	+	+
(8) *Epioblasma obliquata* (Raf., 1820)			O	O	O	O	
(9) *Pleurobema clava* (Lam., 1819)				+	+	+	+
(10) Quadrula cylindrica (Say, 1817)					+	+	+

TABLE 3 (CONT.)

Species	other Great Lakes			Erie Subbasins		Ohio Subbasins	
	LM	LH	LSC	LE	Mau	Wab	Ohio
Erie Fauna (cont.):							
(11) *Ellipsaria lineolata* (Raf., 1820)					O	+	+
(12) *Ligumia subrostrata* (Say, 1831)					O	+	
(13) *Uniomerus tetralasmus* (Say, 1831)				O		+	+
Northern Atlantic Slope Fauna:							
(1) *Elliptio complanata* (Lightfoot, 1786)		+	+	O			O
(2) *Ligumia nasuta* (Say, 1817)		+	+	+	+		

Species erroneously attributed to the Lake Erie Basin (1) *Fusconaia subrotunda* (Lea, 1831), (2) *Lampsilis abrupta* (Say, 1831), (3) *Leptodea leptodon* (Raf., 1820), (4) *Megalonaias nervosa* (Raf., 1820), (5) *Obovaria retusa* (Lam., 1819), (6) *Potamilus capax* (Green, 1832), and (7) *Potamilus ohiensis* (Raf., 1820).

TABLE 3 (CONT.)

The Great Lakes Fauna (1) *Anodontoides ferussacianus* (Lea, 1834), (2) *Lampsilis cardium* (Raf., 1820), (3) *Lampsilis siliquoidea* (Barnes, 1823), (4) *Ligumia recta* (Lam., 1819), (5) *Lasmigona complanata* (Barnes, 1823), (6) *Lasmigona compressa* (Lea, 1829), (7) *Pyganodon grandis* (Say, 1824), (8) *Strophitus undulatus* (Say, 1817), and (9) *Utterbackia imbecillis* (Say, 1829).

The Central Great Lakes Fauna (1) *Actinonaias ligamentina* (Lam., 1819), (2) *Alasmidonta marginata* Say, 1818, (3) *Alasmidonta viridis* (Raf., 1820), (4) *Amblema plicata* (Say, 1817), (5) *Elliptio dilatata* (Raf., 1820), (6) *Epioblasma triquetra* (Raf., 1820), (7) *Fusconaia flava* (Raf., 1820), (8) *Lasmigona costata* (Raf., 1820), (9) *Leptodea fragilis* (Raf., 1820), (10) *Obliquaria reflexa* Raf., 1820, (11) *Obovaria olivaria* (Raf., 1820), (12) *Pleurobema coccineum* (Conrad, 1834), (13) *Potamilus alatus* (Say, 1817), (14) *Quadrula pustulosa* (Lea, 1831), (15) *Quadrula quadrula* (Raf., 1820), and (16) *Villosa iris* (Lea, 1829).

1997) and Lake Ontario (Metcalfe-Smith *et al.*, 1998) to the west and east, respectively. A few species of the Central Great Lakes Fauna also occur in Lake Ontario. The ubiquity of these faunas limits their biogeographic value as regards the Lake Erie region.

The four mussels found in both the Erie and Michigan basins but that are absent from the Lake Huron drainage comprise the (3) Erie-Michigan Fauna (Table 3). The (4) Erie Fauna is composed of those 13 Erie Basin mussels that are absent from Lake Michigan. Finally, *Elliptio complanata* and *Ligumia nasuta*, although both occur in the Erie Basin, were not present historically in the adjacent Interior Basin (although see Matteson, 1948). These two mussels do occur in the Atlantic drainage of New England, New York, and Pennsylvania (Johnson, 1980; Strayer, 1990) and are considered to be a part of the (5) Northern Atlantic Slope Fauna (Johnson, 1970).

Testing the Glacial Lake Maumee Hypothesis. The distributions of freshwater pearly mussels in Lake Erie and adjacent basins are inconsistent with the Glacial Lake Maumee hypothesis of mussel dispersal. While there can be little doubt that Glacial Lake Maumee drained via the Wabash River, the explicit consequences for dispersal via that route (Table 1) of all 42 Ohio basin mussel species present in the Lake Erie Basin are not evident in their present distributions (Table 3), the geological history of the central Great Lakes, vicariance with other aquatic taxa (Table 4), or what is known of the general late-glacial northern re-advance of freshwater mussels. That is, the consequent of each of the three conditional predictions listed in Table 1 is false. Each of the predictions and data supporting their falsification are discussed in turn below.

Discussion

Prediction 1: All freshwater mussels occurring in the Lake Erie Basin should have similar distributions in adjacent basins. Prediction 1 is false since there are 12 Lake Erie mussel species that are absent from the Lake Huron Basin. Of the 32 species occurring in the Huron Basin, 30 are derived from the Interior Basin (Table 3). The remaining two, *Elliptio complanata* and *Ligumia nasuta*, are clearly migrants from the northern Atlantic Slope (Matteson, 1948; Johnson, 1970, 1980) and shall not be considered further. The 25 Interior Basin mussel species of the Great Lakes and Central Great Lakes faunas that occur in Lake Huron may have entered the Great Lakes via Glacial Lake Maumee or a later Lake Erie stage, or they may have gained accesses to the Huron Basin via Lake Michigan. The source of those mussels is thus unclear as there has been confluence between lakes Michigan and Huron for more than 14,000 years: first through a channel in the Grand-Saginaw Valley (Figure 2) and then later through Lake Michigan outlets in and around the Straits of Mackinac (Hansel *et al.*, 1985). Thus, several thousand years of confluence and multiple potential sources have homogenized the Great Lakes and Great Lakes mussel faunas. Van der Schalie (1941, 1945) demonstrated that confluence in the Grand-Saginaw Valley has influenced the range of at least one mussel species, *Venustaconcha ellipsiformis* (Conrad, 1836), but he did not suggest the timing or the nature of the connection.

The 17 species of the Erie-Michigan and Erie faunas have not suffered the same homogenization. Those mussels occur in the Lake Erie Basin, either generally or limited to the Maumee River drainage, and most also inhabit Lake St. Clair. Only five species of these two faunas occur in Lake Huron (Table 3). All five of these mussels are found in the Lake Erie and Ohio basins but are absent from the Lake Michigan and the upper Mississippi basins (except *Simpsonaias ambigua*, which is present in the Mississippi Basin). This pattern suggests that the eastern Michigan populations of those two faunas entered through a connection (or connections) between Lake Erie and Ohio Basin refugia and not via Lake Michigan. However, the distributions of all 17 Erie-Michigan and Erie mussels indicate that that confluence probably occurred later than the Wabash outlet of Glacial Lake Maumee. This is specifically supported by two observations: (1) the five species of the Erie Fauna present in the Lake Huron Basin suggest their arrival post-dated any confluence with the Michigan basin through the Grand-Saginaw Valley (around 12,500 B.P.; Hansel *et al.*, 1985), otherwise they should also be present in the Michigan Basin; (2) the absence of the remaining mussels of the Erie-Michigan and Michigan Faunas from the near-by Lake Huron Basin is also inconsistent with a model of 14,000 years of dispersal since entering the Erie Basin.

An alternative hypothesis for the distribution of these 17 species is that they entered the Great Lakes via Glacial Lake Maumee, but they have been prohibited from colonizing the Lake Huron Basin by ecological factors such as low temperatures or lack of suitable host fish. However, hypotheses of Glacial Lake Maumee dispersal and present ecological exclusion from the Huron Basin seem mutually exclusive; if mussels can not tolerate the relatively milder conditions of present-day Lake Huron, they should have also suffered from the ice-contact environment of Glacial Lake Maumee. Clarke and Stansbery (1988) suggested that the lower mussel diversity of the upper Great Lakes (*i.e.*, Superior and Huron) was due to the combination of low temperature and low calcium carbonate concentrations in those basins. I have shown elsewhere (Graf and Underhill, 1997) that, in the case of Lake Superior, the depauperate fauna is simply a consequence of the timing of the connection of that watershed with the Mississippi Basin. The issue of host fishes is addressed below.

Prediction 2: The fossil record should not be biased towards any particular assemblage. This prediction is false since the fossil record of the central Great Lakes indicates that in strata older than Nipissing age (6000 to 4000 B.P.), only mussels of the Great Lakes and Central Great Lakes faunas are present (Baker, 1920; Miller *et al.*, 1979, 1985; Miller and Knott, 1989). No dated fossil unionid data are available for Lake Erie. Elsewhere I have argued that the earliest northern re-advance of freshwater mussels during the Late Quaternary was biased toward a few long-term brooding (*i.e.*, bradytictic) species (Graf, 1997c). This is supported by the spatial and temporal distributions of unionids in basins from Glacial Lake Agassiz (in the present-day Nelson River Basin of Minnesota, North Dakota, and central Canada) east to the northern Atlantic Slope. There is no evidence for the presence of any (except *Elliptio complanata*) but these few bradytictic mussel species before roughly 5000 B.P. in the formerly glaciated areas of eastern North America (*e.g.*, Ashworth and Cvancara, 1983; Graf, 1997b). These few species are largely those of the Great Lakes Fauna (= Upper Mississippi River Fauna *sensu* Graf, 1997a), with an analogous assemblage occurring on the northern Atlantic Slope (Graf, 1997c). These data suggest that the majority of mussel species of the Lake Erie Basin may have colonized from southern refugia as late as Nipissing time (6000 to 4000 B.P.), or perhaps more recently.

Prediction 3: The fish should also have colonized the basin via the same routes. If Glacial Lake Maumee was the sole entry point for Lake Erie freshwater mussels, it follows that it must also have been the source of the basin's fishes. Therefore, the same distributional hypotheses should hold for the fishes. However, of the more than 120 fishes inhabiting the Lake Erie Basin, 23 that occur in the

TABLE 4. LIST OF INTERIOR BASIN FISHES THAT OCCUR IN THE LAKE ERIE BASIN BUT THAT ARE ABSENT FROM LAKE HURON (UNDERHILL, 1986; BURR & PAGE, 1986).

Ammocrypta clara Jordon and Meek, 1885
Clinostomus elongatus (Kirtland, 1838)
Erimystax x-punctata (Hubbs & Crowe, 1956)
Erimyzon oblongus (Mitchell, 1814)
Etheostoma spectabile (Agassiz, 1854)
Fundulus notatus (Rafinesque, 1820)
Ictiobus cyprinellus (Valenciennes, 1844)
Lagochila lacera Jordon & Brayton, 1877
Lepisosteus oculatus (Winchell, 1864)
Lepomis humilis (Girard, 1858)
Macrhybopsis storeriana (Kirtland, 1847)
Moxostoma carinatum (Cope, 1870)
Notropis amblops (Rafinesque, 1829)
Notropis buccatus (Cope, 1865)
Notropis dorsalis (Agassiz, 1854)
Notropis photogenis (Cope, 1865)
Noturus miurus Jordon, 1877
Noturus stigmosus Taylor, 1969
Opsopoeodus emiliae Hay, 1881
Percina evides (Jordon & Copeland, 1887)
Phenacobius mirabilis (Girard, 1856)
Phoxinus erythrogaster (Rafinesque, 1820)
Pylodictis olivaris (Rafinesque, 1818)

adjacent Interior Basin are absent from Lake Huron (Table 4; Underhill, 1986; Burr and Page, 1986). Assuming that 14,000 years is sufficient for these fish to disperse from Lake Erie to Lake Huron, their distributions do not support the Glacial Lake Maumee hypothesis of their colonization of Lake Erie.

The distributions of the freshwater mussels and the fishes are not completely independent lines of evidence since the latter are hosts for the larvae of the former. The expectation would be that the distributions of mussels and their host fishes should be closely correlated (Watters, 1992; Vaughn, 2000). Table 5 lists the suspected hosts of the 12 Erie-Michigan Fauna and Erie Fauna unionids absent from Lake Huron and their distributions. Although many of the suspected fish hosts of these mussels do occur in Lake Huron as well as Lake Erie (*e.g.*, *Ameiurus melas*, *Aplodinotus grunniens*, *etc.*), the suspected hosts of other mussels are either unknown in the central Great Lakes (*e.g.*, *C. galactura*) or are generally unknown. The known mussel-host associations do nothing to either refute or support the Glacial Lake Maumee dispersal hypothesis, and more study of the host fishes of Great Lakes mussels is obviously necessary.

TABLE 5. DISTRIBUTION OF FISH HOSTS OF ERIE-MICHIGAN FAUNA AND ERIE FAUNA FRESHWATER MUSSELS ABSENT FROM THE LAKE HURON BASIN. MUSSEL-HOST RELATIONSHIPS ARE TAKEN FROM HOGGARTH (1992; UPDATED BY HOVE, 1995, 1997; O'DEE & WATTERS, 1998). ONLY THOSE ASSOCIATIONS DEMONSTRATED BY ACTUAL TRANSFORMATION ON NATIVE FISHES WERE CONSIDERED. FISH DISTRIBUTIONS ARE TAKEN FROM UNDERHILL (1986). LE = LAKE ERIE BASIN; LH = LAKE HURON BASIN; LM = LAKE MICHIGAN BASIN. + = PRESENT.

mussel species	known hosts	host taxonomy	LM	LH	LE
C. tuberculata	*Ameiurus melas* (Raf., 1820)	Ictaluridae	+	+	+
	Ictalurus punctatus (Raf., 1820)	Ictaluridae	+	+	+
	Pylodictis olivaris (Raf, 1820)	Ictaluridae	+		+
E. lineolata	*Aplodinotus grunniens* Raf., 1819	Sciaenidae	+	+	+
L. subrostrata	*Lepomis cyanellus* Raf., 1819	Centrarchidae	+	+	+
	Micropterus salmoides (Lacepède, 1802)	Centrarchidae	+	+	+
P. clava	*Luxilus chrysocephalus* Raf., 1820	Cyprinidae	+	+	+
	Percina caprodes (Raf., 1818)	Percidae	+	+	+
	Percina maculata (Girard, 1859)	Percidae	+	+	+

TABLE 5 (CONT.)

mussel species	known hosts	host taxonomy	LM	LH	LE
Q. cylindrica	*Cyprinella galactura* (Cope, 1868)	Cyprinidae			
	Cyprinella spiloptera (Cope, 1868)	Cyprinidae	+	+	+
	Notropis amblops (Raf., 1820)	Cyprinidae		+	
T. parvus	*L. cyanellus*	Centrarchidae	+	+	+
T. dociformis	*A. grunniens*	Sciaenidae	+	+	+

U. tetralasmus, E. obliquata, O. subrotunda, T. truncata, and *V. fabalis* hosts unknown

Conclusions and Comments

Independently, these separate lines of evidence (*i.e.*, the freshwater mussel distributions, their fossil record, and vicariant distributions of the fishes) do not provide robust support to confirm or refute the Glacial Lake Maumee dispersal hypothesis. However, taken together they are sufficient to reject the traditional argument that all Ohio Basin Unionidae present in Lake Erie entered via the outflow of Glacial Lake Maumee. While these data suggest that some mussels found their way into the Erie Basin through other mechanisms, they do not point to what those alternative dispersal routes may have been.

The fossil evidence suggests that the mussels of the Erie-Michigan and Erie faunas may have colonized the central Great Lakes as late as 5000 B.P. Both Goodrich (1914) and Hubbs and Lagler (1958) argued that the Maumee and Wabash basins have been periodically connected in recent times, both citing early 20th century floods. Clark (1944) suggested possible Ohio-Erie confluence through the Auglaize Basin; the proximity of the Auglaize to major tributaries of the Ohio River (*e.g.*, the Scioto; see Figure 1) supports that hypothesis. On the opposite side of the Maumee Basin, Gerking (1947) proposed that the Kankakee, the St. Joseph of Lake Michigan, and the St. Joseph of the Maumee were confluent and provided a means of fish dispersal (Figure 1); there was no mention of timing. Further biogeographic studies on a finer scale than applied here will be able to determine the importance of these and other potential tributaries of the Maumee.

Between recent high waters (Goodrich, 1914) and Glacial Lake Maumee, there may have been an additional union of the Maumee and Wabash Basins. Based on the stratigraphy of the Maumee-Wabash Channel near Ft. Wayne, Indiana, Bleuer and Moore (1972: 203) argued that

"...the St. Marys and St. Joseph Rivers continued to flow sluggishly westward down the [Maumee-Wabash Channel] prior to the development of the Maumee River." Thus, the sequence of events they described:

1. Glacial Lake Maumee overflowed the Ft. Wayne Moraine, creating an outlet to the Wabash River.
2. The Glacial Lake Maumee stage ended when Erie Basin outlets were uncovered to the north and east.
3. During the period immediately following the withdrawal of Glacial Lake Maumee, the St. Marys and St. Joseph rivers drained "sluggishly westward" to the Wabash River. Thus, these two tributaries must have changed course to flow into the Maumee sometime *after* the tenure of Glacial Lake Maumee (Figure 2).
4. Any freshwater mussels (and fish) present in the St. Marys and St. Joseph rivers would have been 'captured' into the Maumee Basin.

The geological mechanism for such stream piracy may be headward migration -- the Maumee River eroded its bed in a headward direction until the Wabash was 'beheaded.' Similar scenarios have been proposed for other rivers that flow across glacial terrain (*e.g.*, the Otter Tail and the St. Louis Rivers of Minnesota [Radke, 1992; Graf, 1997b; Ojakangas and Matsch, 1982]). This study of the distribution of freshwater mussels in the Lake Erie and surrounding basins provides yet another example of the possible role of stream capture as a means of expanding the ranges of aquatic organisms.

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